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PRESTRIATE AFFERENTS TO INFERIOR TEMPORAL CORTEX: AN HRP STUDY*

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SUMMARY

The inferior temporal (IT) cortex of 6 macaques was injected with horseradish peroxidase. HRP-labeled cells were found throughout IT cortex itself (outside the injection area) but were not found in the polysensory areas that surround IT dorsally, anteriorly and ventrally. Posterior to IT, labeled cells were found in the anterior parts of prestriate cortex. In one animal, the anterior prestriate region was injected with HRP. Labeled cells were then found in the regions of posterior prestriate cortex that receive direct projections from striate cortex. These results suggest that IT cortex receives information from striate cortex after at least two stages of processing in prestriate cortex.

INTRODUCTION

The inferior temporal cortex (IT) of primates plays an important role in the advanced stages of visual processing. Removal of IT causes severe visual learning impairments without concomitant sensory loss[5,12,13]. IT neurons are exclusively visual, have large, bilateral receptive fields which include the center of gaze and often have complex trigger features[7,15,16]. Recently we have shown that cells with these properties are found throughout cytoarchitectonic area TE but not in adjacent areas[7] (see Fig. 1).

The visual responsiveness of IT neurons is dependent on striate cortex[30]. IT receives an input from striate cortex by way of synapses in prestriate cortex, but the details of this pathway are unknown[21,22,29,33]. Prestriate cortex is made up of several visuotopically organized visual areas. Some of these areas receive a direct projection

* A preliminary account of this study was presented at the 1978 meeting of the Association for Research in Vision and Ophthalmology, Sarasota, Florida[6]. The order of the first two authors was determined alphabetically.

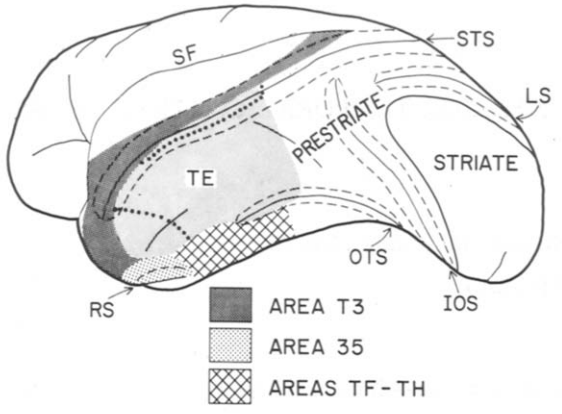

Fig. 1. Ventrolateral view of macaque brain showing area TE and adjacent areas[7,20,37,38]. Occipital and temporal sulci have been opened and their banks shown with dashed lines. The dotted lines separate the anterior and dorsal subregions of TE from the rest of area TE[7]. IOS, inferior occipital sulcus; LS, lunate sulcus; OTS, occipitotemporal sulcus; RS, rhinal sulcus; STS, superior temporal sulcus; SF, Sylvian fissure.

from striate cortex such as V2 (surrounding striate cortex)[10,40] and MT (in the floor of the caudal superior temporal sulcus)[9,15,35,40,42] while others do not[45,46]. Some of these prestriate areas have been reported to be specialized for the analysis of particular stimulus dimensions such as disparity, color or direction of movement[1,18,42,43,45,46].

Earlier studies of the projections from prestriate cortex to IT have generally been based on degeneration following lesions spanning portions of several prestriate visual areas. Furthermore, these studies have usually spared cortex buried in sulci or hidden on the ventral and medial surfaces of the brain. In order to determine which of the prestriate visual areas project to IT, we used a retrograde tracing method, the HRP technique. In this paper we report on projections to IT from temporal, parietal and occipital cortex.

METHODS

Seven *Macaca fascicularis* weighing 3–4.5 kg were used. In 6 animals (M1–M6) horseradish peroxidase (HRP) was injected unilaterally into area TE; one of these (M6) also received a lateral striate lesion. The seventh animal (M7) received a unilateral HRP injection into the anterior prestriate region. Animals were anesthetized with a mixture of halothane, nitrous oxide and oxygen, and the lateral surface of the temporal lobe exposed. In one animal (M2) the injections were made hydraulically; in the other animals they were made iontophoretically. For the hydraulic injections, a 25% solution of HRP (Boehringer, grade I) in saline was injected through a 30-gauge Hamilton microsyringe. Nine injections of 1 μl each were made at the sites shown in Fig. 4. For the iontophoretic injections, a 25% solution of HRP in Tris buffer (pH 7.6) was injected through pipettes with tips of 30–50 μm. In each animal 16–18 injections of 4 μA for 5 min each were made 1–1.5 mm below the pia mater (see Figs. 3–7).

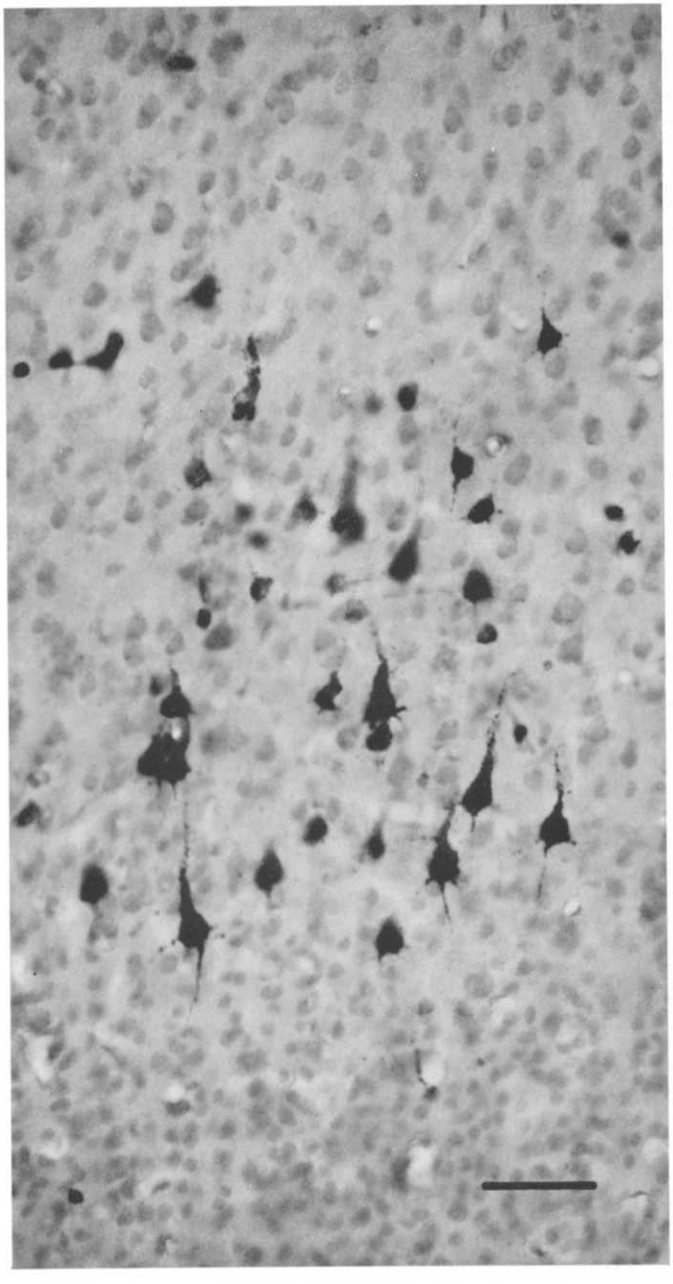

Fig. 2. Labeled cells (dark) in anterior prestriate cortex following HRP injections in IT. Labeled cells are located in layer 3, inferior occipital gyrus. Bar = 50 μm.

Following a survival period of 2 (M3, M6, M7), 3 (M1, M2, M5), or 5 (M4) days, the animal was perfused transcardially with 300 ml saline followed by 2000 ml of 1.25% glutaraldehyde and 1% paraformaldehyde in 0.1 M phosphate buffer (pH 7.4)[11]. The fixative was then washed out by further perfusion with 2000 ml of 10%

sucrose in phosphate buffer at 4 °C[32]. The brain was then removed, photographed, and stored overnight in sucrose buffer at 4 °C. The following day the brain was cut into 40 μm sections and every fifth section processed with Mesulam's benzidene dihydrochloride[25] (BDHC, cases M1–M6) or tetramethyl benzidene[24] (TMB, case M7) methods. Both of these methods yield a blue reaction product and are considerably more sensitive than the standard diaminobenzidene method[24,25]. Following counterstaining with neutral red, the temporal, parietal, and occipital neocortex was examined for labeled cells. Examples of labeled cells are shown in Fig. 2. The distribution of labeled cells was charted with the aid of an X–Y plotter electronically coupled to the microscope stage.

The lateral striate lesion (in animal M6) was made by subpial aspiration 6 days prior to sacrifice. Sections adjacent to the ones processed with BDHC were stained for anterograde degeneration using method I of Fink and Heimer[8].

RESULTS

The center of each injection site contained a dense core of dark blue reaction product surrounded by a light blue halo of diffuse reaction product. The limits of the

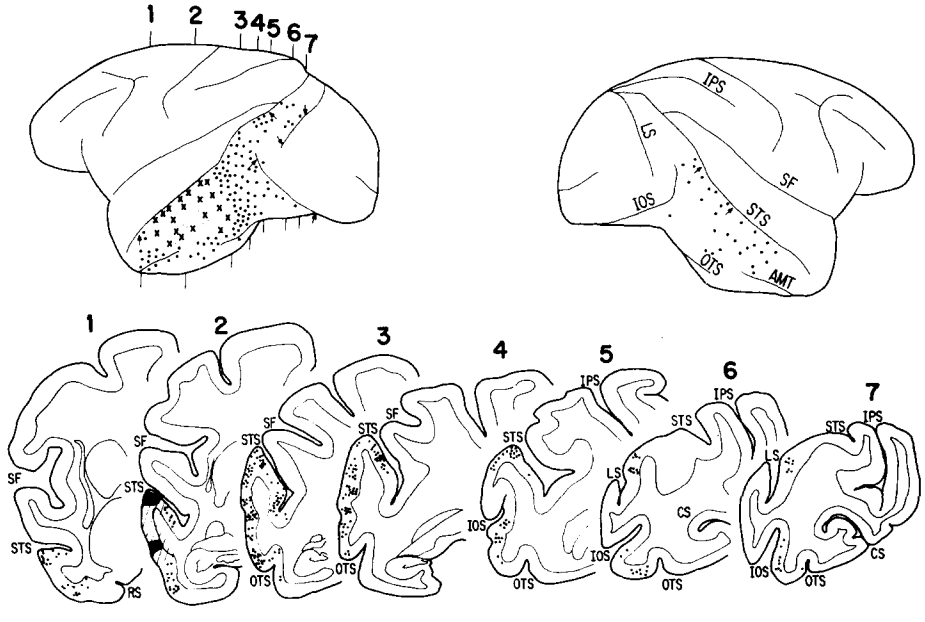

Fig. 3. Case M1. Distribution of labeled cells following HRP injections into IT. In the lateral reconstructions, '×s' indicate the sites of the iontophoretic injections, and the shaded area indicates the area of spread of HRP. The relative density of labeled cells is indicated by dots, and arrows delimit where labeled cells were found in a bank of a major sulcus. Labeled cells were also found in both banks of the anterior middle temporal sulcus and in the occipitotemporal sulcus, mainly in the lateral bank. In the coronal sections, the black areas indicate the sites of the injections, the hatched areas indicate the spread of HRP, and each dot represents an individual labeled cell. AMT, anterior middle temporal sulcus; CS, calcarine sulcus; IPS, intraparietal sulcus. See also legend to Fig. 1.

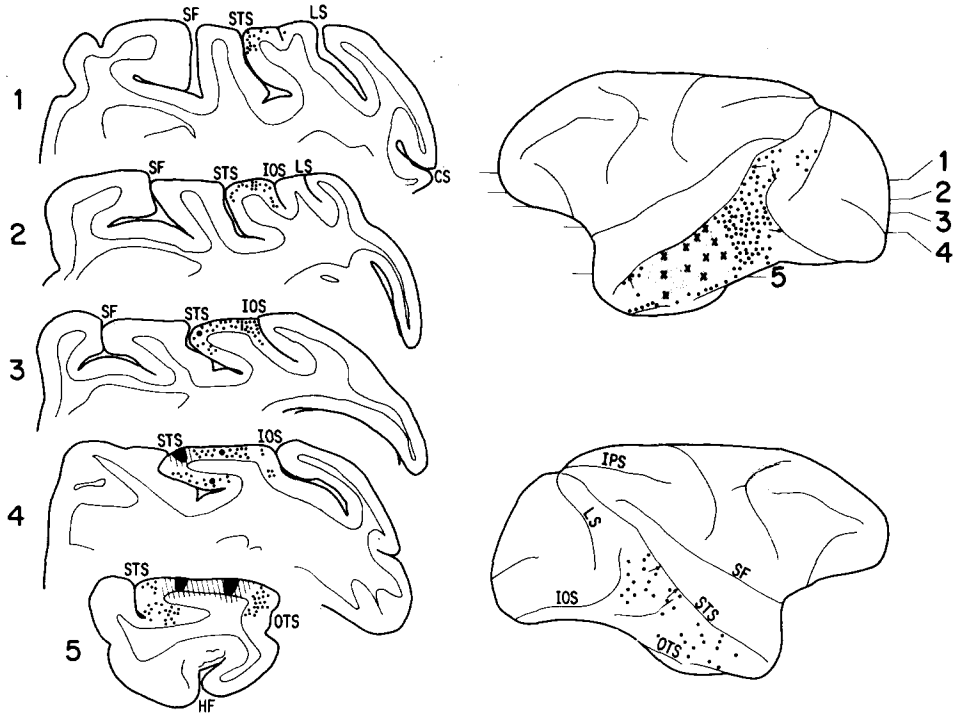

Fig. 4. Case M2. Distribution of labeled cells following HRP injections into IT. Injections were made hydraulically rather than iontophoretically as in case M1. In the horizontal sections, the large dots each represent 20 labeled cells and the small dots individual cells. HF, hippocampal fissure. See also legend to Figs. 1 and 3.

diffuse reaction product defined the 'injection area'. With survival times of 2 or 3 days, the cores of the iontophoretic injections measured about 1 mm in diameter, and the cores of the hydraulic injections were about 1.5 mm. Between the injection sites labeled cells were found in all layers of the cortex, and the light blue reaction product filled the extracellular space and 1–3 mm of the underlying white matter. The spread of the reaction product was more extensive with the hydraulic injections. All damage produced by the pipettes or needles was confined to the cortex, and, therefore, it is unlikely that HRP was incorporated by axons running beneath the cortex[17,23,39].

For the IT injections (all of which were processed with the BDHC method) the distribution of labeled cells was qualitatively the same at the different survival times. The animals with 3-day survival time had the greatest number of labeled cells, and the animal with 5 days the least.

Ipsilateral projections to IT

Cases M1–M4 (Figs. 3 and 4). All of the injections in these cases were located within the central part of cytoarchitectonic area TE[38]. The injection areas were located between 8 mm and 20 mm anterior to the ascending limb of the inferior occipital sulcus. Dorsally, the injections extended to the lip of the superior temporal sulcus and

ventrally to within 2 mm of the occipitotemporal sulcus. Since the distribution of labeled cells was similar in all four cases, only the results from case M1 (Fig. 3) will be described in detail.

Anterior to prestriate cortex, labeled cells were found in area TE, but not across the boundaries with adjacent cytoarchitectonic areas. Anteriorly, the region containing labeled cells extended to almost the temporal pole; however, no labeled cells were found in the thick polar cortex, which is included within Jones and Burton's[20] cytoarchitectonic area T3 (see Fig. 1). Dorsally, the cortex containing labeled cells extended into the lower bank of the superior temporal sulcus (STS), close to the border of TE with area T3 (Fig. 3; sections 1 and 2). However, there were very few labeled cells in the most dorsal portion of TE, i.e. in the floor of STS (see Fig. 1). Ventrally, labeled cells were found up to the border of area TE with areas 35b[37] and TF-TH[37,38] (Fig. 3; sections 1, 2 and 3). Thus, there were no labeled cells in the regions surrounding IT rostrally (area T3), dorsally (area T3) or ventrally (areas 35b and TF-TH). We have previously shown that neurons in each of these surrounding areas are sensitive to somesthetic and auditory as well as to visual stimuli, in contrast to IT which is exclusively visual[3,7].

While some of the labeled cells in IT may have become labeled by direct spread of HRP from the injection area, most of them were probably due to intra-IT connections. This is suggested both by their restriction mainly to layers 3 and 5 (see below) and by the close correspondence between the region containing labeled cells and the boundaries of IT which have been established physiologically and cytoarchitectonically[7].

From the posterior border of IT, the region containing labeled cells continued into the anterior parts of prestriate cortex. A heavy concentration of labeled cells was located anterior to the tip of the inferior occipital sulcus, stretching from the floor of STS to the occipitotemporal sulcus (Fig. 3; sections 3 and 4). Within this region, the distribution of labeled cells was somewhat irregular or patchy. Although originally included within area OA by von Bonin and Bailey[38], Iwai and Mishkin have termed this area TEO[19]. Our physiological recordings in this region have established that most of it is devoted to the foveal and parafoveal visual field[7,15].

More posteriorly within prestriate cortex, the region containing labeled cells was split by the inferior occipital sulcus into dorsal and ventral parts. Dorsally, labeled cells were situated in the lower bank of STS and the prelunate gyrus. As sections were traced posteriorly, the labeled cells in STS gradually moved laterally towards the lip of the sulcus (Fig. 3; sections 4–6). Labeled cells on the prelunate gyrus were most heavily concentrated along the lips of the lunate sulcus and STS (Fig. 3; sections 5 and 6). Ventral to the tip of the inferior occipital sulcus, labeled cells were found in the anterior bank of the sulcus and along the lip.

In contrast to the heavy concentration of labeled cells in anterior prestriate cortex, there were apparently no labeled cells in the two major striate-recipient regions of prestriate cortex[4,35,40]. The first region lies adjacent to the striate border and includes the posterior banks of the lunate and inferior occipital sulci. Most of this region contains a visuotopically organized area called V2[10,36,40]. This region was

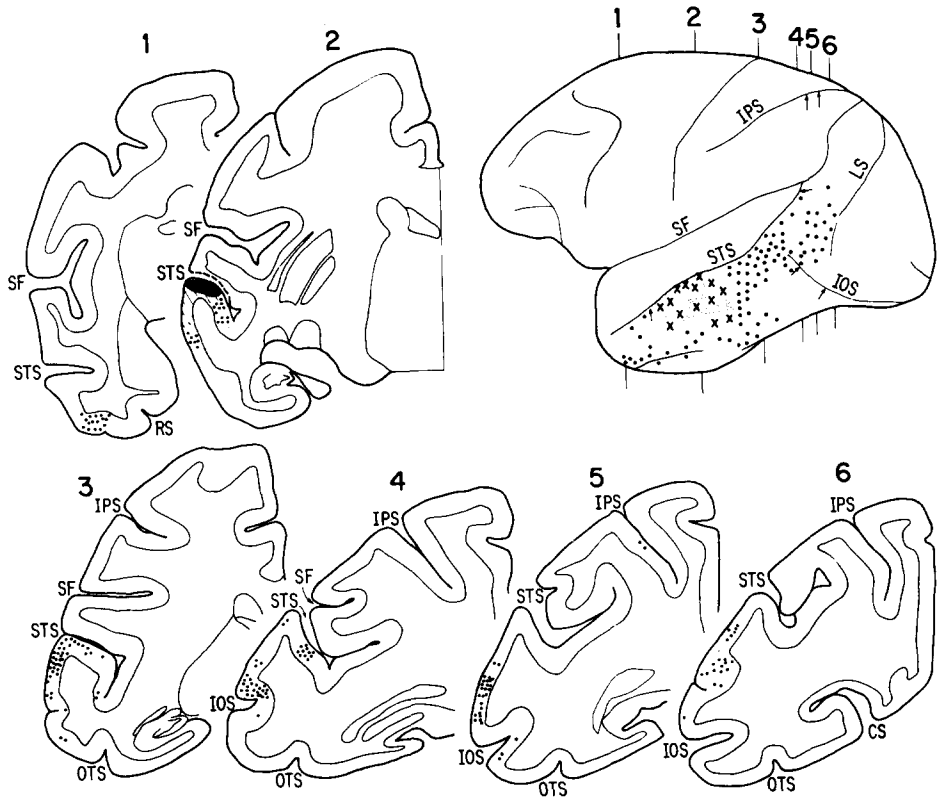

Fig. 5. Case M5. Distribution of labeled cells following HRP injections into IT. The dashed line in section two indicates the portion of the upper bank of STS removed to facilitate the injections into STS. See also legend to Figs. 1 and 3.

clearly free of labeled cells. The second region, the middle temporal area, or MT, lies deep within STS[9,15,35,40,42,43]. It has been called the STS 'movement area' by Zeki[46]. While there were many labeled cells in the lateral part of the posterior bank of STS, these appeared to avoid MT. This was confirmed in case M6 (below).

For comparison, case M2 is shown in Fig. 4. Although similar to the other cases, case M2 had the lightest concentration of labeled cells on the prelunate gyrus.

Case M5 (Fig. 5). In case M5, unlike the previous ones, two injections were made into the ventral bank of STS after removal of a small part of the overlying dorsal bank. Additional injections were made on the lateral surface, but the injection area did not extend as far ventroposteriorly as in cases M1–M4.

The distribution of labeled cells in M5 was basically similar to cases M1–M4. Anterior to prestriate cortex, labeled cells were confined to the uninjected parts of IT. Within prestriate cortex, labeled cells were confined to the anterior parts. Only two major differences from the other cases were noted. The first was the presence of a few labeled cells in the ventral bank of the intraparietal sulcus. These cells were located near its posterior end, a few millimeters from the ventral lip (Fig. 5; section 5). Several

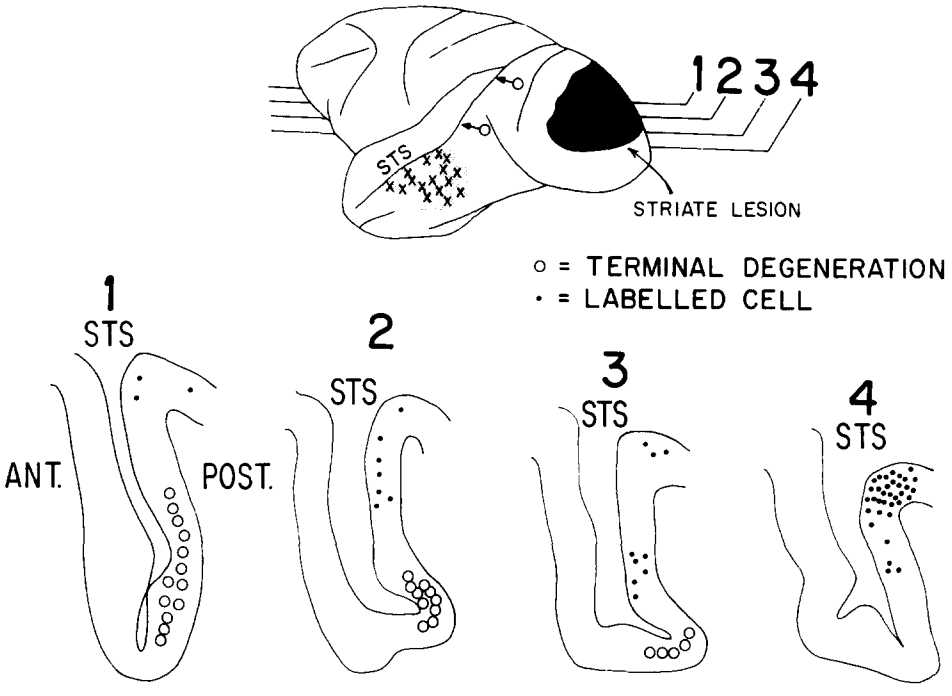

Fig. 6. Case M6. Distrubution of labeled cells and terminal degeneration in the superior temporal sulcus following combined HRP injections into IT and lateral striate lesion. Adjacent sections were processed with either selective silver or HRP histochemistry techniques and then superimposed. Arrows delimit where terminal degeneration was found in the ventral bank of STS.

studies have shown that this part of the intraparietal sulcus receives projections from lateral prestriate cortex[21,22,29]. The second difference was the relative paucity of labeled cells on the ventrolateral surface of the brain, both within IT and prestriate cortex. This may be related to the restricted ventro-posterior extent of the injection area.

Case M6 (Fig. 6). In cases M1–M5, the region containing labeled cells in prestriate cortex avoided the striate-recipient area in the lunate and inferior occipital sulci. However, we could not be certain that no labeled cells were located in striate-recipient area MT in the superior temporal sulcus. Therefore, in case M6, a lateral striate lesion was made 4 days prior to the HRP injections into IT. The anterograde degeneration from this lesion was used to identify the central representation of the visual field within MT. (The peripheral representation of MT is located in the floor of STS[9,15,35] far from the region containing labeled cells, and was, therefore, unnecessary to identify with this procedure.) The labeled cells resulting from the HRP injections were used to identify the cortex projecting to IT.

The distribution of labeled cells in prestriate cortex was similar to that in cases M1–M4. The distribution of terminal degeneration in STS was similar to that which has been described by Zeki[40] and others[4,21,22]. Fig. 6 shows that there was no overlap between the area containing labeled cells and the area containing terminal degenera-

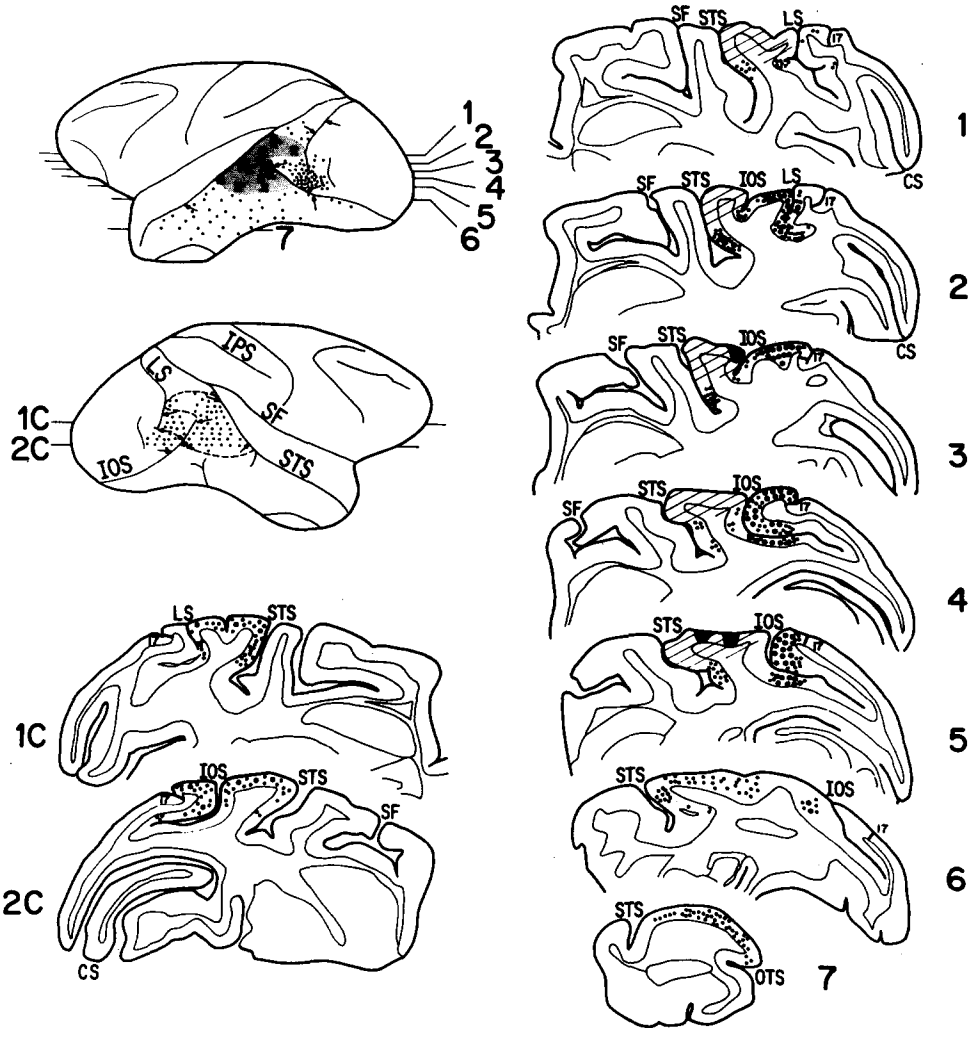

Fig. 7. Case M7. Distribution of labeled cells following HRP injections into part of anterior prestriate cortex. In the ipsilateral hemisphere, labeled cells were also found in the banks of the lunate sulcus between the arrows and the ventral tip. In the contralateral hemisphere the dashed lines indicate the cortex homotopic to the injection area. See also legend to Figs. 1, 3 and 4.

tion. At every level, the terminal degeneration was located medial to the labeled cells. Therefore, it appears that MT does not project directly to IT.

In addition to the degeneration in STS, the lateral striate lesion resulted in heavy terminal degeneration in the posterior banks of the lunate and inferior occipital sulci, similar to that described by others[4,40]. Since, as in cases M1–M4, there were no labeled cells in the posterior banks of the lunate or inferior occipital sulci, this striate-recipient region also probably does not project directly to IT. Other studies have indicated that additional striate-recipient cortex may in some animals extend a short distance onto

the prelunate gyrus, and thus, close to the region in which we observed labeled cells[4,44]. Due to some superficial damage to parts of the prelunate gyrus (caused while re-opening the dura mater for the HRP injections) we were unable to determine if there was a complete absence of degeneration in this region.

Contralateral projections to IT

There were a relatively small number of labeled cells located in the hemisphere contralateral to the IT injections (Figs. 2, 3 and 4). Within IT, labeled cells were most dense in the cortex directly opposite the injection area. Within prestriate cortex labeled cells continued posteriorly along the dorsal surface of the middle temporal gyrus and into the adjacent bank of STS, ending at about the level of the inferior occipital sulcus.

Projections to anterior prestriate cortex

Case M7 (Fig. 7). Following the HRP injections into IT, the heaviest concentrations of labeled cells were located at the anterior end of the prelunate gyrus and in the cortex anterior to the inferior occipital sulcus. To determine the source of inputs to this area, we injected it with HRP. The region injected included the anterior end of the prelunate gyrus, extended about 9 mm in front of the inferior occipital sulcus, and included a small posterior part of area TE. We had previously established with electrophysiological recordings in this animal that neurons in the area directly injected had receptive fields located within 2° of the center of gaze.

The heaviest concentrations of labeled cells following these injections were located in the ipsilateral posterior prestriate region, within a few millimeters of the border of striate cortex. In the most dorsal sections (Fig. 7; section 1), there were only a few labeled cells in the posterior bank of the lunate sulcus. As sections were traced ventrally labeled cells rapidly increased in number, occupying both banks of lunate sulcus near its tip and spreading into the inferior occipital sulcus (Fig. 7; section 2). Ventral to the tip of lunate sulcus, the cortex containing labeled cells stretched from less than 1 mm from the striate border to about midway down the posterior bank of the inferior occipital sulcus (Fig. 7; sections 3 and 4). By contrast, this region, adjacent to the striate border and including the posterior banks of the lunate and inferior occipital sulci, was essentially free of labeled cells after the injections confined to IT. Previous studies have indicated that this area receives projections from the central representation in striate cortex[4,40,44]. It includes at least the representation of the fovea in V2 and possibly of other, yet undefined prestriate visual areas[10,40,44].

In addition to the labeled cells in the region adjacent to striate cortex there were also labeled cells in the same regions that contained labeled cells after injections confined to IT, viz the prelunate gyrus, the ventral bank of STS, the anterior bank of the inferior occipital sulcus, and in cytoarchitectonic area TE. In the prelunate gyrus and adjacent anterior lip of lunate sulcus, dorsal to the injection area, labeled cells were relatively sparse (Fig. 7; sections 2,3 and 4). Within STS, there were a moderate number of labeled cells near the bottom of the lower bank. While these labeled cells in STS continued further medially than the labeled cells following IT injections, they still may avoid area MT.

Within the anterior bank of the inferior occipital sulcus, there was a discrete, densely concentrated group of labeled cells which gradually moved out to the lip of the sulcus as sections were traced ventrally (Fig. 7; sections 4–6). This area containing labeled cells appeared at least partially coextensive with the area in the inferior occipital sulcus that contained labeled cells following IT injections. In the temporal lobe, labeled cells were found throughout most of cytoarchitectonic area TE, but spared the most rostral part of TE near the temporal pole and the most dorsal part of TE in the floor of STS.

In summary, following HRP injections into part of the anterior prestriate region, labeled cells were found ipsilaterally (1) in the posterior striate-recipient region (which contains V2), (2) in the prelunate gyrus, (3) in the ventral bank of STS, (4) in the anterior bank of the inferior occipital sulcus, and (5) throughout most of IT.

In the contralateral hemisphere, labeled cells were found in two areas (Fig. 7; sections 1C and 2C). One area was directly opposite the injection area, i.e. the anterior end of the prelunate gyrus, the adjacent bank of STS, and the cortex immediately anterior to the tip of the inferior occipital sulcus and a few millimeters into its anterior bank. The other area containing labeled cells was located just anterior to the foveal representation of striate cortex. As was true ipsilaterally, labeled cells filled the cortex between the tips of the lunate sulcus and the inferior occipital sulcus and, as sections were traced ventrally, stretched from less than 1 mm from the striate border to more than midway down the posterior bank of the inferior occipital sulcus. This area contains the foveal representation of V2 and perhaps other areas[10,40,44].

Laminar distribution of labeled cells

Following both the IT and the anterior prestriate injections, the laminar distribution of labeled cells followed a similar pattern. In cortical regions posterior to the injection area, i.e. between the injection area and striate cortex, labeled cells were located predominantly in the lower and middle parts of layer 3 (see Fig. 2). In cortical regions anterior to the injection area, i.e. between the injection area and the temporal pole, the distribution of labeled cells gradually shifted to the infragranular layers, especially layer 5. For example, following the IT injections the labeled cells in anterior prestriate cortex were located primarily in layer 3; however, within the uninjected parts of area TE there were an increased number of labeled cells in layer 5, and in the most rostral part of TE the number of labeled cells in layers 5 and 6 outnumbered those in layer 3. In prestriate cortex, Rockland and Pandya found a similar pattern of rostrally directed projections originating from the supragranular layers and caudally directed projections originating from both supragranular and infragranular layers[31]. Following both the IT and the anterior prestriate injections, labeled cells in the contralateral hemisphere were located exclusively in layer 3, especially the middle and lower parts.

DISCUSSION

The HRP technique for demonstrating anatomical connections has several limitations. One risk is that spurious projections will arise from spread of HRP into surrounding areas or from uptake by damaged axons of passage[17,23,39]. A com-

plementary risk is that some connections will be missed due to the failure of HRP to be taken up or transported by some axonal systems[27]. Thus, it is encouraging that most of the anatomical connections we have demonstrated with HRP are consistent with previous studies based on anterograde techniques.

The present results indicate that IT receives a major input from the anterior part of prestriate cortex and an apparently very minor input (to the STS portion of IT) from an area in the intraparietal sulcus. Previous anterograde studies also found projections from part of the anterior prestriate region to IT and also a projection from within the ventral bank of the intraparietal sulcus to the deep STS portion of IT[33]. Furthermore, our HRP data indicate that IT does not receive projections from posterior prestriate areas, including V2, from prestriate cortex on the ventral or medial surface, or from MT. Anterograde studies have also failed to find projections to IT from either the most posterior prestriate areas[41] or from the medial prestriate cortex[33]. While there are no studies of the efferent projections of MT in the macaque, the apparently homologous area in the marmoset does not appear to project to the inferior temporal region[34].

The present results also demonstrate projections from the foveal representations of the posterior striate-recipient areas to the portions of anterior prestriate cortex that project heavily to IT. These projections were previously found in anterograde anatomical studies by Zeki[41] and Kuypers et al.[22].

In several ways the projections to IT fit nicely with the response properties of units in IT and surrounding areas. First, IT units are exclusively visual[7,16], and IT cortex receives projections only from exclusively visual cortical areas and not from the polysensory cortex[2,3,7] that surrounds it on three sides. Second, IT receptive fields always include the center of gaze[7,16], and IT cortex receives its projections primarily from the portions of anterior prestriate cortex in which the central visual field is represented[7,15]. Third, the visual responsiveness of IT neurons in the ipsilateral visual field depends on projections it receives through the interhemispheric commissures[14], and the present study indicates that the contralateral IT and anterior prestriate cortex are the sources of these projections. Fourth, within IT cortex there is an anterior region near the temporal pole and a dorsal region in the floor of STS (see Fig. 1) in which the receptive fields are much larger than in the rest of IT. Since neither of these portions of IT apparently receive (nor send, cf. case M7) direct projections from prestriate cortex[33], their properties may be primarily determined by a converging input from the rest of IT.

Finally, it is interesting to note that following HRP injections into IT, the distribution of labeled cells in anterior prestriate cortex appears similar to the pattern of degeneration found following corpus callosum section[26,28]. The suggestion that callosal terminations tend to be restricted to cortex containing a representation of the vertical meridian[36] is consistent with the finding that IT receives projections primarily from the central representations of the anterior prestriate areas.

Pathways to IT

The present results indicate that IT cortex receives information from striate

cortex after at least two 'stages' of processing in prestriate cortex. The first stage includes the posterior prestriate region which receives a direct projection from striate cortex. The second stage includes the areas of anterior prestriate cortex that receive projections from the striate-recipient areas and project directly to IT. The composition of these two stages is not yet clear. The first stage, the posterior striate-recipient region, includes at least area V2. The second stage, the anterior prestriate region (which projects to IT directly) is less well understood. Electrophysiological studies of this region have indicated that much of it is concerned with the central visual field, and that it contains more than one visuotopically organized area[7,15,36,43,45,46]. One of these areas lies on the lip and upper part of the superior temporal sulcus immediately adjacent to MT[9,15,43] and may receive projections from MT (as does the apparently homologous area in the marmoset[34]). If so, it would provide a route for MT to send information to IT. Another area located within the anterior prestriate region is an area Zeki calls the 'V4 complex'[45,46]. This area occupies the prelunate gyrus and anterior bank of lunate sulcus but its exact borders and topography have not been determined.

What we have termed the two 'stages' of processing between striate cortex and IT probably includes most of the prestriate visual areas, particularly their central representations. Thus, the visual pathway to IT is a highly convergent one. If the multiplicity of prestriate visual areas represents a division of labor in the analysis of stimulus features, perhaps this convergent pathway to IT is a mechanism for integrating these analyses. The complex trigger features of IT neurons and the high-order pattern discrimination impairments which follow IT lesions are consistent with this notion that IT plays a role in integrating the results of stimulus analysis in the prestriate visual areas.

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